THE FERN GENERA VITTARIA AND TRICHOMANES IN THE NORTHEASTERN UNITED STATES[1]

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Abstract. *Vittaria* is reported from 5 counties in Pennsylvania; *Trichomanes* from 24 counties in Connecticut, Maryland, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, and Vermont. All are new state records except *Trichomanes* in Massachusetts. These ferns occur as gametophytes only, but in large conspicuous populations in crevices and grottos of moist, non-calcareous rock outcrops in canyon topography. The northernmost distribution of *Trichomanes* has not been established, but may parallel that of the oak-hickory forest type. *Vittaria* was not found north of the southern terminus of Pleistocene glaciation; its northern distribution may have been truncated by that event. *Vittaria* sites in northwestern Pennsylvania are well north of apparently suitable glaciated habitats in eastern Pennsylvania wnich house *Trichomanes* but not *Vittaria*.

Field botanists of the southern Appalachian Mountain and Plateau regions of the Eastern U.S. are familiar with the occurrence of conspicuous populations of fern gametophytes totally devoid of the sporophyte phase of the fern life cycle. Best known of these is the Appalachian *Vittaria* gametophyte which produces dense, vivid green colonies often dominating the flora of heavily shaded, moist outcroppings of non-calcareous rocks (Farrar, 1978). Less familiar but equally common are the filamentous gametophytes of the genus *Trichomanes* which form velvety cushions and tufts in the same habitats as *Vittaria* (Farrar, 1967; Wagner & Evers, 1963). Gametophytes of both genera have the ability to reproduce themselves vegetatively by means of gemmae and thus exist independently of and beyond the range of their sporophyte counterparts. Sporophytes of *Vittaria* are totally absent from Eastern U.S. uplands, and gametophytes of *Trichomanes* are known far north of the range of sporophytes of *Trichomanes petersii* and *Trichomanes boschianum* (with northernmost occurrences in Sevier Co., Tennessee and Hocking Co., Ohio respectively). It was, in fact, the recent discovery of *Trichomanes* gametophytes in Massachusetts (McAlpin & Farrar, 1978) that prompted this study.

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In considering the origin of the Appalachian *Vittaria* gametophytes, Farrar (1978) proposed that they were possibly relicts of a Tertiary subtropical flora. In support of this hypothesis he cited the basic tropical affinity of the genus, the morphological and physiological differentiation of the Appalachian plants from all other known species of *Vittaria*, and the restriction of their occurrence to rock exposures predating and lying south of the borders of Pleistocene glaciation. It was also suggested that *Trichomanes* shared many of these characteristics and may have experienced a similar history.

The distribution of *Vittaria* and *Trichomanes* in the Northeastern U.S. has not been carefully studied previously. Since appropriate habitats here are abundant and continuous through the southern terminus of Pleistocene glaciation, this is an important area in which to investigate the factors limiting the distribution of these unusual plants and providing clues to their origin. They also constitute significant new additions to the floras of the northeastern states in which they occur.

METHODS

Field search for gametophytes of *Vittaria* and *Trichomanes* was conducted in portions of all states north of the Virginias, except Delaware and Rhode Island. Sites for investigation were identified through consultation with local field botanists and naturalists, analysis of physiographic maps, and checking of herbarium records of plants commonly associated with the gametophytes in more southern locations. Available time permitted investigation of only a fraction of the sites so identified. Herbarium vouchers were collected and prepared for deposit in the herbaria of Iowa State University, The New York Botanical Garden, and Millersville State College of Pennsylvania.

RESULTS AND DISCUSSION

Vittaria gametophytes were collected from 6 sites in 5 counties of Pennsylvania, and *Trichomanes* gametophytes were collected from 32 sites in 24 counties of Pennsylvania, Maryland, New Jersey, New York, Connecticut, Massachusetts, Vermont, and New Hampshire. These constitute new state records for all states listed except Massachusetts. A listing of collection sites and habitat substrates is given in Appendix 1.

Habitats of *Vittaria* and *Trichomanes* gametophytes in the Northeast are very similar to those in the Southeast: heavily shaded, moist outcroppings of non-calcareous rock. A significant difference is that occurrence of the gametophytes in the north seems to require development of these habitats on a larger scale. Gorges must be deeper and narrower, cliffs and waterfalls must be higher, and sites in general must offer greater buffering from climatic extremes than is required to support these plants in the south.

This extreme of habitat and microclimate specificity is well illustrated by the habitat of *Vittaria* at its northernmost station at Jake's Rocks in Warren County, Pennsylvania (Figure 1). This cave-like habitat was created by the cleavage and slumping of a huge sandstone block from an undercut cliff face. The massive, porous sandstone provides continuous moisture while moderating temperature through radiation and blockage of wind currents. Sufficient light (about 100 ft. c.) penetrates the "cave" opening to allow growth of *Vittaria*.

Trichomanes may also require wetter habitats in its northernmost localities. In the Catskill Mountains of New York and Green Mountains of Vermont it was collected only from crevices of rocks which were saturated with moisture, even during the relatively dry period

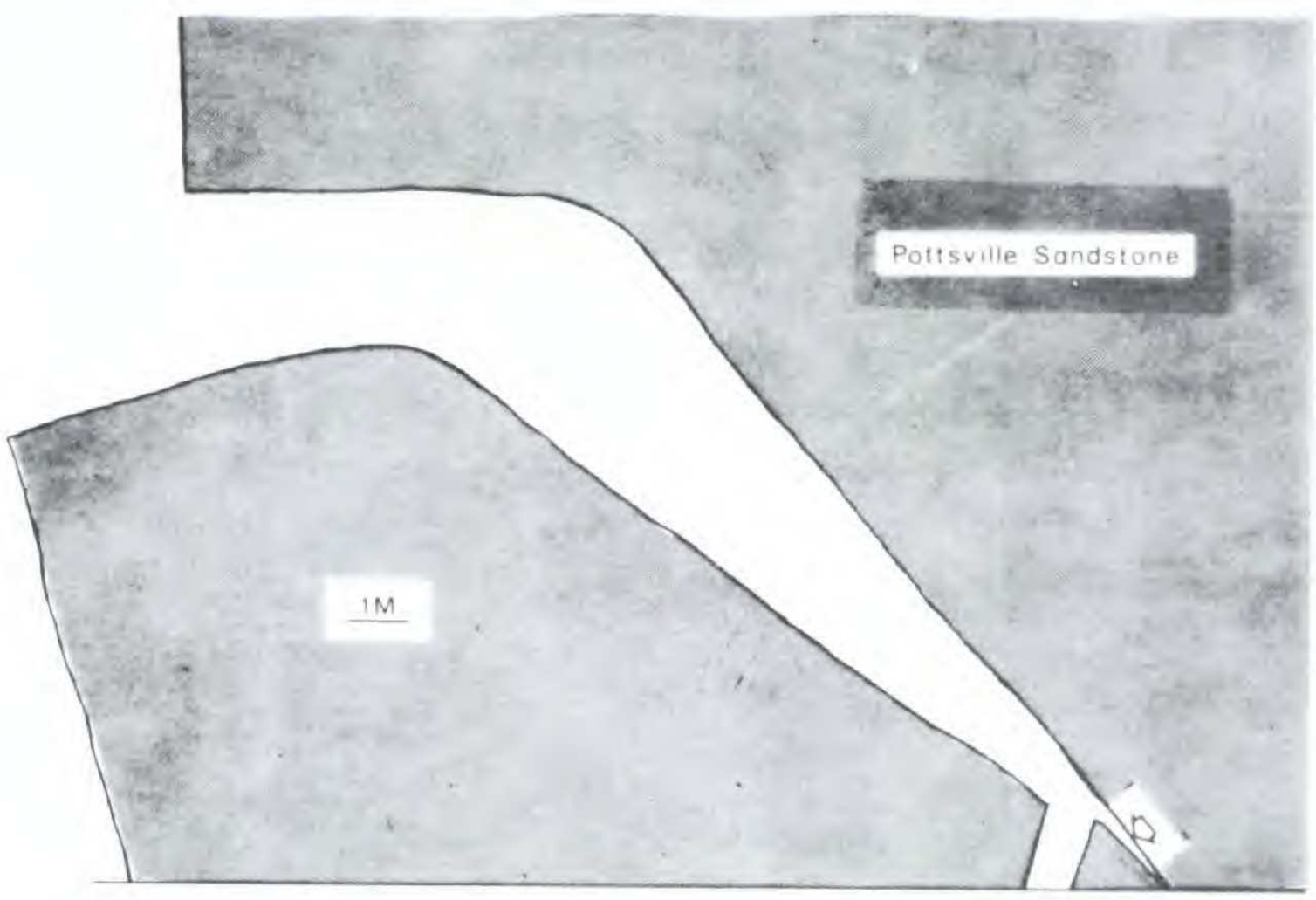

Figure 1. Diagrammatic cross section of the habitat of Appalachian *Vittaria* gametophytes at Jake's Rocks on the Allegheny Reservoir in Warren Co., Pennsylvania. Arrow indicates the microhabitat of *Vittaria*.

when collections were made. By contrast, in Pennsylvania and more southern areas, *Trichomanes* gametophytes often occur in habitats that are periodically quite dry.

The currently known distribution of *Vittaria* and *Trichomanes* in the Northeastern U.S. is presented in Figure 2. The distribution of *Trichomanes* clearly is not governed by the limits of glaciation. The northern limit of *Trichomanes* was not determined in this study as no sites north of the collections in New York and Vermont were investigated. A search for *Trichomanes* in habitats with suitable physical characteristics in the White Mountains of New Hampshire (Franconia Notch area) and Maine (Grafton Notch area) was unproductive. However, forest vegetation of these sites is decidedly more northern than the Central Hardwoods—Oak-Hickory forest (Westveld, 1956; Little, 1971) typical of *Trichomanes* sites. On the

Figure 2. The known distribution of *Vittaria* (stars) and *Trichomanes* (dots) in the northeastern United States. Each symbol represents a county in which the plants were collected. Hatched lines represent the approximate southern limits of Wisconsin (upper line) and Illinoian (lower line) glaciation.

basis of its association with this forest type, a northern limit for *Trichomanes* may be predicted to occur in the mountains of southernmost Quebec.

Vittaria gametophytes were not found in any habitats covered by Wisconsin glaciation. They were found in habitats just beyond the southern terminus of Wisconsin glaciation, and in one site, approximately one kilometer within the boundary of Illinoian glaciation (Gray, 1960). Some *Vittaria* sites are as far north as glaciated sites harboring *Trichomanes* but not *Vittaria*. Since the two genera have nearly identical habitat requirements, frequently sharing the same habitat, it is reasonable to conclude that Pleistocene glaciation has influenced the current distribution of *Vittaria*.

In considering the origin of gametophytes of *Vittaria* and *Trichomanes*, it is important to analyze the nature of their habitats and probable means of dispersal. Their habitats are invariably situated within canyon-like topography and surrounded by a dense mature forest canopy. The microhabitats in which they grow are crevices or grottos deeply recessed under cavernous rock outcrops. Wind currents in these microhabitats are minimal so that wind dispersal of propagules into or out of these habitats seems unlikely. More plausible dispersal agents are the variety of insects and other invertebrates which actively seek out these same habitats.

Another aspect of their distribution suggests that they are not presently being dispersed beyond their immediate habitats. They are not found in man-made habitats such as roadcuts, tunnels, bridges or quarries, although these often present all conceivable combinations of light and moisture with appropriate substrate, and are in proximity to existing populations. Many such habitats have been in existence 100 years or more.

If the gametophytes are not currently dispersing and thus not invading adjacent available habitats, when did they reach their current northeastern distribution? In the case of *Trichomanes*, this was certainly post-Pleistocene, perhaps during a hypsithermal period (Cushing, 1965; Davis, 1965) when a warmer climate may have facilitated northward migration. At this time, sporophytes of *Trichomanes* may also have extended their distribution northward into this area and contributed to the spread of the gametophytes.

A pre-Pleistocene distribution of *Vittaria* appears to have been truncated by Pleistocene glaciation. This conclusion is evidenced by the coincident northern limits of the plants and southern limit of

glaciation from southern Indiana[1] to eastern Pennsylvania. This coincidence holds despite the fact that habitats near the more northerly areas of the glacial terminus appear much less favorable to warm temperate plants than do some more southerly habitats lying north of glaciation. For example, the high, exposed rim rocks of the Allegheny reservoir in unglaciated northwestern Pennsylvania support populations of *Vittaria* whereas the more protected narrow canyons and waterfalls of Rickets Glen and the Delaware Water Gap of glaciated cental and eastern Pennsylvania contain abundant *Trichomanes* but not *Vittaria.*

Could the absence of *Vittaria* within the glaciated area be attributed to glacial alteration of habitats rendering them permanently unsuitable for these plants? In the Appalachian Mountains there is little probability of this surmise as the mountain topography was not greatly altered by glaciation, and glacial drift has been largely removed from upland areas through subsequent erosion (Muller, 1965; Schafer and Hartshorn, 1965; Thornbury, 1965). Common acidiphilic fern associates of *Vittaria,* e.g. *Asplenium montanum,* and *Trichomanes* gametophytes, and mosses such as *Hookeria acutifolia* also show no limitations to unglaciated areas (Crum & Anderson, 1981; Wherry, 1942).

In glaciated areas west of the Appalachian Mountains, calcareous tills generally overlie sandstone outcrops of the type suitable for *Vittaria* in unglaciated areas (Goldthwait, et al., 1965; Wayne & Zumberge, 1965; Thornbury, 1965) and such outcrops are less frequent and less continuous than they are beyond the glacial terminus. These factors are significant, but do not alone explain the absence of *Vittaria* in this area. *Trichomanes* occurs in Montgomery County, Indiana, suggesting suitability of habitat there, approximately 25 km within Wisconsin glaciation. *Vittaria* occurs in Martin Co., approximately 100 km from the Montgomery Co. site and just beyond the Illinoian glacial boundary.

In Lawrence Co., Pennsylvania, *Vittaria* gametophytes occur in great abundance on Pottsville sandstone approximately 1 km within Illinoian glaciation and about 1 km beyond the Wisconsin glacial limit. Some post-Illinoian migration of the gametophytes has

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[1]This study has yielded new county records for *Vittaria* gametophytes in Martin and Perry Counties, Indiana and Fairfield County, Ohio. It was previously known from Crawford County, Indiana and Hocking and Jackson Counties, Ohio.

obviously occurred, perhaps made possible by the continuity of suitable habitats along Slippery Rock Creek from this area to well south of glacial limits.

Similarly, in Hocking and Fairfield counties of Ohio, *Vittaria* is abundant on the common and continuous outcrops of Pottsville sandstone to within 1 km of the glacial terminus. However, it is absent from the relatively isolated outcrops of the same substrate in Licking Co., Ohio, 60 km to the northeast, although habitats here support populations of *Trichomanes* gametophytes, *Asplenium pinnatifidum,* and the acidophilous mosses *Hookeria acutifolia* and *Bryoxiphium norvegicum,* all frequent associates of *Vittaria.* These observations suggest that a large geographical extent and linear continuity of suitable habitats are important determinants of the occurrence of *Vittaria,* perhaps operating through probability of habitat continuity over time as well as provision of migration routes requiring minimal transport distances.

It is difficult to explain this distribution of the Appalachian *Vittaria* gametophytes except by assuming a very limited dispersal capacity and consequently a Pleistocene occurrence very near the glacial terminus. The latter is not unlikely considering the bryophyte-like growth form of *Vittaria,* its ability to tolerate freezing (Farrar, 1978), and the strong climatic moderation afforded by the cave-like habitats of these plants (Fig. 1). Similar rock shelters in Alabama, Illinois, and Missouri contain remains of human habitation which have been dated at more than 9000 years b.p. (Jennings, 1968). Clearly these habitats are stable and very likely persisted with little modification throughout the Pleistocene. In such habitats a frequent associate of *Vittaria* in the northern, unglaciated portions of the Appalachian Plateau is the sword moss, *Bryoxiphium norvegicum.* Steere (1937) described this moss as exhibiting a relict distribution pattern of a species which thrived near the periphery of pleistocene glaciers.

In summary, it seems likely that both *Trichomanes* and *Vittaria* reached pre-Pleistocene and possibly interglacial northern limits more or less coincident with the distribution of the Central Hardwood forests of eastern North America. *Trichomanes* has regained this distribution during post-Pleistocene time, possibly during an interval warmer than the present. *Vittaria,* by contrast, appears to have migrated very little beyond the areas to which it was restricted by Pleistocene glaciation. The greater post-Pleistocene migratory

success of *Trichomanes* may be related to the more northerly occurrence of sporophytes of this genus.

Many prospective northeastern sites for these ferns remain uninvestigated. *Trichomanes* may be expected wherever sizeable outcrops of non-calcareous rocks occur throughout the range indicated in Figure 2, and further significant range extensions are likely to be documented in the northeastern U.S. and possibly in southeastern Canada. *Vittaria* likely occurs throughout unglaciated Pennsylvania and possibly in unglaciated portions of New York and New Jersey. Our conclusions regarding the history and mobility of *Vittaria* do not exclude the possibility of its chance occurrence within the limits of Pleistocene glaciation.[2] However, present information strongly suggests that if found in such areas, *Vittaria* there will not approach the abundance or frequency of its occurrence in unglaciated areas.

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[2]Note added in proof: Collections of *vittaria* gametophytes have recently been made in Lake and Geauga Counties in northeastern Ohio by Allison Cusick of the Ohio Department of Natural Resources. The plants were collected from Sharon Conglomerate exposed along the Lake Erie watershed. This site is approximately 80 km north of the Wisconsin glacial terminus and constitutes the first documented occurrence of *Vittaria* within the boundaries of Wisconsin glaciation.

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APPENDIX 1

LIST OF COLLECTIONS[1]

Vittaria[2]

PENNSYLVANIA: **Huntingdon Co.:** Orbisonia Gap, Juniata and Tuscarora sandstone, 81-9-20-6, 81-9-20-7. **Lancaster Co.:** Kelley's Run, Wissahickon schist, 81-9-22-6; Tucquan Glen, Wissahickon schist, 81-10-2-5. **Lawrence Co.:** McConnell's Mill—Gorge of Slippery Rock Creek, Pottsville sandstone, 81-10-21-4. **Warren Co.:** Jake's Rocks on Allegheny Reservoir, Pottsville sandstone, 81-10-20-1. **York Co.:** Otter Creek, Wissahickon schist, 81-9-22-12.

Trichomanes[2]

CONNECTICUT: **Litchfield Co.:** Campbell Falls—gorge south of falls, schist, 81-10-17-2; Kent Falls, granite-gneiss, 81-10-17-3. MARYLAND: **Cecil Co.:** Susquehanna River—east side, 1 km south of Pa. state line, Peters Creek Schist, 81-9-23-1. MASSACHUSETTS: **Franklin Co.:** West of Mt. Toby along Hwy 47, 5 km north of Sunderland, Triassic conglomerate and shale, 81-10-16-1. NEW HAMPSHIRE; **Cheshire Co.:** Chesterfield Gorge, quartzite, 81-10-15-1. NEW JERSEY: **Warren Co.:** Delaware Water Gap—Van Campen's Brook, Bloomsburg shale and siltstone, 81-9-27-2. NEW YORK: **Green Co.:** 1 km south of Westkill on Hwy 42, Catskill sandstone, 81-10-10-1. **Schoharie Co.:** Minekill Falls, sandy shale, 81-10-10-3. **Sullivan Co.:** Frost Valley, Catskill sandstone, 81-10-9-5. **Ulster Co.:** Frost Valley, Catskill sandstone, 81-10-9-8. **Westchester Co.:** Mianus River Gorge, schist, 81-10-9-2. PENNSYLVANIA: **Blair Co.:** Bell's Gap, Pocono sandstone, 81-9-19-1. **Butler Co.:** Jennings Environmental Education Center, Pottsville sandstone, 81-10-21-1. **Cambria Co.:** Bell's Gap, Pocono sandstone, 81-9-19-3. **Carbon Co.:** Hickory Run, Pocono sandstone, 81-9-25-1. **Huntingdon Co.:** Juniata River—junction of US 22 and Pa 829, Catskill sandstone and shale, 81-9-20-1; Orbisonia Gap, Juniata sandstone, 81-9-20-5. **Lancaster Co.:** Kelly's Run, Wissahickon schist 81-9-22-8; Pequea River, Wissahickon schist, 81-10-2-8; Furnace Hills—Seglock Run, Triassic conglomerate and shale, 81-9-30-1. **Lawrence Co.:** McConnel's Mill—Gorge of Slippery Rock Creek, Pottsville sandstone, 81-10-21-7. **Luzerne Co.:** Rickett's Glen—Kitchen Creek Falls, Pocono sandstone, 81-10-18-1. **Monroe Co.:** Delaware Water Gap—Slateford Creek, Martinsburg shale, 81-9-27-1. **Pike Co.:** Bushkill Falls, Marine Bed shale and sandstone, 81-9-26-1; Dingman's Falls, Marine Bed shale and sandstone, 81-9-26-8. **Tioga Co.:** Colton Point—Pine Creek Gorge, Catskill sandstone, 81-10-19-1. **York Co.:** Susquehanna River at Accomac, Chickies quartzite. 81-9-30-1; Otter Creek, Wissahickon schist, 81-10-12-4. VERMONT: **Addison Co.:** 2 km west of Ripton, quartzite, 81-10-12-1; Moss Glen, schist, 81-10-12-2. **Washington Co.:** Mad River Glen, schist, 81-10-12-4.

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[1]Collection numbers are those of Farrar.

[2]All specimens are gametophytes only.